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Genetic variation in peanut leaf maintenance and transpiration recovery from severe soil drying

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ABSTRACT

Peanut (*Arachis hypogaea* L.) is an important food crop that is often grown in areas prone to intermittent drought. After drought is relieved, plant recovery from soil drying is an important factor for continued productivity. While recovery can involve a multitude of physiological processes, transpiration is one of the most important for carbon fixation. Two greenhouse experiments and a field experiment were conducted to screen and evaluate a total of 19 peanut genotypes for transpiration recovery and leaf maintenance after experiencing a drying cycle. In the greenhouse experiments, plants were allowed to transpire all available transpirable soil water from their pots before being re-watered. The transpiration of plants was measured in subsequent days and a visual rating scale was used to rate leaf maintenance on plants. Significant differences were detected among genotypes for both transpiration recovery and leaf maintenance, and superior genotypes were identified for both traits. The superior genotypes included ICGV 86015, TMV 2, PI 497579 and PI 404020 in the greenhouse. In the field, a regression between stomatal conductance before and after re-watering gave an estimate for recovery of stomatal conductance. Breeding lines N05006 and SPT 06-07 had the greatest estimated stomata conductance recovery in the field. Genotypes which recovered poorly in the greenhouse also had low estimated recovery in the field.

1. Introduction

Peanut (*Arachis hypogaea* L.) is usually grown on sandy soils with low water-holding capacity, and often grown without irrigation. In non-irrigated fields, long dry periods between rainfall events may cause plants to experience severe water-deficit stress. This can often lead to substantial yield losses or even complete crop failure.

Three stages in plant response to soil drying have been proposed by Sinclair and Ludlow (1985). Stage I occurs when plants are unstressed, stomatal conductance is at maximum and water uptake is unhindered. Stage II occurs as the soil dries and plants begin to close stomata for longer periods during the day. Plants maintain the water balance between water uptake and water loss, resulting in a reduction in overall transpiration concurrent with decreasing soil water. These first two stages have been well documented in peanut, and genotypic differences in response to soil drying have been reported (Devi et al., 2009; Shekoofa et al., 2013). Some peanut genotypes initiated decreases in transpiration when soil water was as high as 70% of available water and others when available soil water was as low as 25%. Comparison of genotypic differences in recovery from 30% available water (Puangbut et al., 2010) may well reflect differences in the threshold for the decrease in transpiration.

Stage III begins when the soil dries further, exhausting transpirable soil water. At this point, plants are unable to control water loss through any further stomatal closure and regulation of water loss is by the vapor resistance of the leaf epidermis and the difference in vapor pressure between the leaves and atmosphere (Muchow and Sinclair, 1989). During severe water-deficit, a plant's ability to survive and subsequently recover after re-watering may depend on its ability to delay leaves from reaching a lethal dehydration state by limiting water loss from the leaf epidermis (Flower and Ludlow, 1986; Sinclair and Ludlow, 1986; James et al., 2008a). The ability to recover from a severe dry period upon re-watering and to maintain productivity resulting in acceptable yields would be beneficial to farmers.

Genetic variation for plant recovery from severe water-deficit (Stage III) has been shown in soybean (James et al., 2008b), among species of bentgrass (*Agrostis capillaries* L.; *Agrostis stolonifera* L., *Agrostis canina* L.) (DaCosta and Huang, 2007) and among various legumes (Sinclair and Ludlow, 1986; Likoswe and Lawn, 2008). Recovery from stress has also been reported for peanut but

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Table 1
For all peanut genotypes evaluated in this study, information on the origin, type or species, use, whether they have been released, and in which experiment they were used is provided in this table.

Genotype	Use	Type/species	Origin	Release	Greenhouse/field
N05006	Breeding line	Virginia	NCSU	Unreleased	Field, GH 1
SPT 06-07	Breeding line	Species-derived[a]	NCSU	Unreleased	Field, GH 1
Bailey	Commercial	Virginia	NCSU	Released	Field, GH 1
Georgia Green	Commercial	Runner	Univ. of GA	Released	Field, GH 1
HTS 02-05	Breeding line	Species-derived[a]	NCSU	Unreleased	Field, GH 1, 2
N05008	Breeding line	Virginia	NCSU	Unreleased	Field, GH 1, 2
N04074FCT	Breeding line	Virginia	NCSU	Unreleased	GH 1
ICGV 86015	Commercial	Spanish	ICRISAT	Released	GH 1
NC-V11	Commercial	Virginia	NCSU	Released	GH 1
HTS 02-01	Breeding line	Species-derived[a]	NCSU	Unreleased	GH 1
Phillips	Commercial	Virginia	NCSU	Released	GH 1
PI 433525	Germplasm	Peruviana	Peru	–	GH 1
CHAMPS	Commercial	Virginia	VPIandSU	Released	GH 1
PI 576636	Germplasm	Hirsuta	Mexico	–	GH 1
PI 404020	Germplasm	Spanish	Senegal	–	GH 1
PI 497579	Wild species	*A. stenosperma*	Brazil	–	GH 1, 2
ICGV 86388	Commercial	Spanish	ICRISAT	Released	GH 1, 2
TMV 2	Commercial	Spanish	Tamil Nadu, India	Released	GH 1, 2
PI 298639	Wild species	*A. batizocoi*	Bolivia	–	GH 2

[a] Can be traced back to a wild species within a few generations.

none of the studies allow a comparison among genotypes under severe stress. Awal and Ikeda (2002) studied only a single cultivar. Lauriano et al. (2004) withdrew watering of three peanut genotypes grown in pots for 9 d to impose a severe drought. The difficulty is that by withholding water for a fixed number of days for all plants ignores the possibility that for several reasons the rate and severity of stress may have differed among plants. Consequently, the differences they observed in recovery from stress may be confounded by plants being at differing levels of stress.

This study was undertaken to compare the recovery from severe water-deficit stress among up to 19 peanut genotypes in greenhouse and field experiments. A key feature of these experiments was to compare genotypes experiencing a similar degree of physiological stress. An initial greenhouse experiment screened eighteen peanut lines for variation in recovery from a soil drying cycle. A second greenhouse experiment was undertaken with five lines selected from the first greenhouse experiment plus an additional peanut wild species to confirm that variation exists within the peanut germplasm. A third experiment was conducted in the field under rain-shelters to evaluate the recovery from water-deficit treatments using measurements of stomatal conductance in six selected peanut genotypes.

2. Materials and methods

Two greenhouse experiments were conducted at N. C. State Univ., Raleigh, NC and a field experiment at the Tidewater Agric. Res. and Ext. Ctr. (TAREC) in Suffolk, VA to evaluate the recovery of a total of nineteen peanut genotypes from Stage III stress. The genotypes were chosen based on drought tolerance, origin, commercial status, and seed availability. Detailed information for all genotypes is presented in Table 1.

2.1. Plant culture and treatments

Greenhouse Experiment 1 (GH 1) was designed to evaluate the recovery of eighteen peanut genotypes after re-watering from Stage III stress based on a visual rating of the plant canopy and transpiration recovery. Three seeds from each genotype were sown in 2.8-L, 16.5-cm tall plastic pots on 15 April 2011. The pots were filled with a sandy loam soil (69% sand, 18% silt, 13% clay) amended with 20 g of pulverized $CaCO_3$ to neutralize soil acidity. Two weeks after sowing, pots were thinned to one plant to achieve uniformity in plant size. One week after thinning, 1.02 g of fertilizer (5–13–20, $N–P_2O_5–K_2O$, The Scotts Company LLC, Marysville, OH) dissolved in 88 ml of water was added to each pot. Each genotype was represented by a total of twelve replicate pots that were eventually evenly assigned to three watering treatments. The greenhouse was sprayed with a pesticide once every two weeks to control thrips. Later in the season flowers were removed daily to keep plants in the vegetative stage. Mean daily temperatures in the greenhouse averaged 27–32 °C.

Greenhouse Experiment 2 (GH 2) was designed to impose a prolonged severe stress (Stage III) on plants to compare with results obtained in GH 1. Five genotypes with contrasting response to re-watering after Stage III stress from GH 1 were selected and an additional genotype, PI 298639 (*Arachis batizocoi* Krapov. & W.C. Greg) was added to widen the genetic diversity of the material evaluated in GH 2. Seeds were sown on 8 June 2011 and maintained as in GH 1. The only difference was that the soil did not need to be fertilized or limed because the soil was recycled from GH 1. Each genotype was represented by twelve replicate pots evenly assigned to three treatments. Mean daily temperatures in the greenhouse averaged 28–32 °C.

2.2. Drying cycle

In both GH 1 and GH 2, plants were grown under well-watered conditions for about four weeks. On the day prior to starting the drying cycle, pots were over-watered and allowed to drain overnight. The following morning all pots were enclosed in white plastic bags with the opening of the bag bunched around the base of the plant and firmly held together by twist ties. A small plastic tube was also inserted in the opening for irrigating the pot. The bags ensured that no evaporative water loss occurred and any water loss from the pots was *via* transpiration. All pots were weighed after placing them in the bags to determine initial weight. All pots were individually weighed on a daily basis usually between 1300 and 1600 EST and watered between 1600 and 1700 EST.

To avoid rapid soil dehydration, water was added to pots if necessary to restore daily net transpirational water loss to 70 g. Well-watered plants for each genotype were re-watered daily to restore pot weight to 100 g below the initial weight. The 100-g deficit was to prevent saturated conditions in the well-watered pots.